

DIRECTIONAL SELECTION ON INITIAL FLOWERING DATE IN *PHLOX DRUMMONDII* (POLEMONIACEAE)¹

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The fitness effects due to initial flowering date in *Phlox drummondii* were determined for three populations in central Texas (USA) over 3 yr (1990–1992). Mean fitness (seed set) always decreased with the later initiation of flowering. The likelihood of a plant fruiting differed with flowering date in five of the six instances (population by year combinations). Though plants that initiated flowering later tended to have spent more time in the vegetative stage and tended to die later in the year than did earlier flowering plants, this was not sufficient to overcome the reproductive penalties of flowering late. Plants that initiated flowering later in the season spent less time in the adult phase and were smaller. The mean number of flowers, fruits, and seeds per flowering plant always decreased with later flowering. Fruit set was negatively correlated with flowering date in four of the six population by year combinations. Nonparametric fitness functions were used to summarize predicted fitness among different initial flowering dates for each population on a yearly basis. Predicted mean fitness always declined nonlinearly with later flowering; the earliest flowering plants always had the highest predicted fitness. These fitness functions describe directional selection for the early initiation of flowering.

Key words: flowering date; directional selection; nonlinear fitness functions; *Phlox drummondii*; Polemoniaceae.

The life history of a species may be regarded as a comprehensive adaptive trait that has been molded by natural selection to maximize fitness. In plants, a fundamental aspect of the individual's life history that determines fitness is flowering date. Individuals in the same population typically begin to flower at different times. When the transition from vegetative plant to reproductive plant occurs has a substantial impact on plant fitness. The fitness differences between plants that initiate flowering at different times is often manifested through its effects on a suite of reproductive traits: flower size (Ashman, 1992), flower number (Schemske, 1977; Zimmerman and Gross, 1983; Flanagan and Moser, 1985; De Jong and Klinkhamer, 1991), inflorescence number (Schemske, 1977; De Jong and Klinkhamer, 1991), duration of plant's flowering period (Schmitt, 1983; Marquis, 1988), age at first reproduction (Lotz, 1990), the timing of fruiting (Widen, 1991a), fruit number (Primack, 1980; Flanagan and Moser, 1985; Mullins and Marks, 1987; Agren and Willson, 1992), fruit set (Primack, 1980; Kephart, 1987; Marquis, 1988; Agren and Willson, 1992), reproductive effort (Primack and Antonovics, 1982), and the onset of seed dispersal (Lacey, 1982).

Individual differences in the timing of flowering may be due to several environmental factors: (1) temperature (e.g., Schemske, 1977; Schemske et al., 1978; Primack, 1980; McGuire and Armbruster, 1991), (2) rainfall (e.g., Augspurger, 1981; Marquis, 1988), (3) light availability (e.g., Marquis, 1988), (4) plant size (e.g., Schemske,

1977; Schmitt, 1983; Marquis, 1988; Lotz, 1990; Widen, 1991a), (5) herbivore attack (e.g., Augspurger, 1981; Zimmerman and Gross, 1983; English-Loeb and Karban, 1992), or (6) plant density (e.g., Augspurger, 1981; Schmitt, 1983). Individual differences in the timing of flowering also may be genetically determined (e.g., Cooper, 1959; Lawrence, 1963; Hiesey, Nobs, and Bjorkman, 1971; Jones, 1971; Westerman, 1971; McIntyre and Best, 1978; Jain, 1979; Carey, 1983; Troyer and Larkin, 1985; Widen, 1991a; and reviewed in Murfet, 1977). When the timing of flowering is genetically determined, differences in the fitness of plants that begin to flower at different dates can be directly related to their genotype. For either case, environmental or genetic determination of flowering, the adaptive value of a flowering date can be inferred from the differences in fecundity between plants known to have initiated flowering at different dates in the same season and at the same site, hereafter referred to as flowering date.

In many species, plants that begin to flower early in the flowering season have enhanced reproductive performance (e.g., *Claytonia virginica*, *Erythronium albidum*—Schemske et al., 1978; *Leptospermum scoparium*—Primack, 1980; *Solidago juncea*—Gross and Werner, 1983; *Spartina anglica*—Mullins and Marks, 1987; *Glycine max*—Lin and Nelson, 1988; *Plantago major*—Lotz, 1990; *Viscaria vulgaris*—Kwak and Jennersten, 1991; *Geranium maculatum*—Agren and Willson, 1992) and directional selection for earlier flowering is inferred from these results. In other species, plants that initiated flowering in synchrony with the population were typically the most fit (e.g., *Dentaria laciniata*, *Isopyrum biternatum*—Schemske et al., 1978; *Fouquieria splendens*—Waser, 1979; *Hybanthus prunifolius*—Augspurger, 1981; *Linanthus androsaceus*—Schmitt, 1983; *Aralia nudicaulis*—Flanagan and Moser, 1985; *Piper arieanum*—Marquis, 1988; *Cynoglossum officinale*—De Jong and Klinkhamer, 1991; *Senecio integrifolius*—Widen, 1991b), and stabilizing selection for an intermediate flowering date inferred.

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In contrast, late flowering plants were usually the most fit for only a few plant species, (e.g., *Discaria toumatou*—Primack, 1980; *Catalpa speciosa*—Stephenson, 1982; *Polemonium foliosissimum*—Zimmerman and Gross, 1983; *Solidago canadensis*, *S. graminifolia*, and *S. nemoralis*—Gross and Werner, 1983; *Aralia nudicaulis*—Flanagan and Moser, 1985; *Asclepias incarnata*, and *A. syriaca*—Kephart, 1987); and directional selection for later flowering was proposed from these data. At present there is little evidence for disruptive selection on flowering date (e.g., *Impatiens pallida*—Stewart and Schoen, 1987).

One purpose of this investigation was to determine the effects of different flowering dates on individual fitness in an annual plant species, *Phlox drummondii*. We describe the effects of the initial flowering date on lifetime reproductive performance (i.e., seeds per flowering plant) at multiple sites over multiple years for the naturally defined time available to each individual for reproduction. Though this measure of fitness considers only the female component, and not male contribution via pollen, it is a robust estimate of fitness in the field. Kelly (1992) has similarly determined the effects of different flowering dates on individual fitness in another annual plant species, *Chamaecrista fasciculata*. In contrast to our first purpose, most studies of the fitness consequence of different flowering dates evaluated only perennial plant species (Schemske, 1977; Primack, 1980; Lacey, 1982; Primack and Antonovics, 1982; Schmitt, 1983; Zimmerman and Gross, 1983; Flanagan and Moser, 1985; Kephart, 1987; Mullins and Marks, 1987; Marquis, 1988; Lotz, 1990; Widen, 1991b; De Jong and Klinkhamer, 1991; Agren and Willson, 1992; Ashman, 1992). With perennial plants, even if multiple years and sites are surveyed, the fitness effects ascribed to flowering date represent a fraction of the plant's lifetime reproductive performance over an haphazardly defined time period.

A second purpose of this research was to explicitly summarize the relation between the timing of flowering and fitness with fitness functions. There are various quantitative methods to measure selection, each with its own advantages and disadvantages (Wade and Kalisz, 1990). Here the fitness function that related individual fitness to flowering date was determined using the nonparametric curve fitting method of Schluter (1988). This method of regression is nonparametric in that it does not require an a priori model for the quantitative relationship between a given phenotype and fitness. The graphical depiction of the relationship between flowering date and fitness allows one to visualize the adaptive nature of this trait and describe the form of selection as: directional, stabilizing, or disruptive.

Together, these set the stage for understanding the evolutionary potential in the timing of flowering in *Phlox drummondii*. Though many studies have inferred the pattern of phenotypic selection on this trait, only Widen (1991b) and Kelly (1992) have summarized the relation between flowering day and seed set using fitness functions. As the genetic composition of a population may be modified by the action of natural selection (directly or indirectly) on this trait, it is necessary to measure the direction and intensity of phenotypic selection on initial flowering date in natural populations in order to under-

stand the potential for evolution in the timing of flowering and its genetically correlated traits (e.g., reproductive effort—Primack and Antonovics, 1982; and references in Rathcke and Lacey, 1985).

MATERIALS AND METHODS

The plant—*Phlox drummondii* Hook. (Polemoniaceae) is a winter annual native to central and southern Texas (USA). This self-incompatible (gametophytic), outbreeding, hermaphrodite grows abundantly in sandy fields and along disturbed roadsides (Levin, 1993). Populations typically contain hundreds to thousands of flowering plants pollinated by butterflies and moths. Individual plants usually begin to bloom in the spring, at any time from March through May. The adult phase of life lasts around 6 wk (Leverich and Levin, 1979; Kelly, 1994; Kelly and Levin, 1997). Though growth is indeterminate, plants typically produce only five to six flowers and a flower senesces within 7 d (Leverich and Levin, 1979). From these five to six flowers a plant usually forms three to four fruits (Kelly, 1994; Kelly and Levin, 1997). The fruits normally contain two or three seeds dispersed by explosive capsule dehiscence. Individuals ordinarily die after maturing their fruits, or when rainfall decreases and temperatures increase in late May at the end of the flowering season (Leverich and Levin, 1979; Kelly, 1994; Kelly and Levin, 1997).

Field study—The following studies were conducted over 3 yr (1990, 1991, and 1992) at three sites in central Texas (USA): Montopolis (Travis County), Bastrop (Bastrop County), and Luling (Caldwell County). In 1990 the study was conducted at Montopolis, Bastrop, and Luling. Four plots (1.5 × 1.5 m per plot) spaced 0.5 m apart were arranged in a checkerboard pattern over a total area of 12.25 m². The four plots were permanently laid out at the site before natural seedling emergence. In 1991, the study used the same sites as in the previous year; however, the Montopolis site was eliminated after being vandalized. The methods employed in 1991 were the same as in 1990, with the addition of color coded wires to mark the initiation of each inflorescence within the plant. In 1992, four smaller plots (1 × 1 m²) spaced 1 m apart were permanently marked at Bastrop. These plots occupied a 9.0 m² area; otherwise, the methods employed in 1992 were the same as in 1991.

All *Phlox* plants used in this study flowered. Each plant's initial flowering date was marked with a color-coded wire; this provided a record of that season's flowering phenology. Though all sites were surveyed at least once per week (to monitor *Phlox* flowering, fruiting, or mortality) surveys were often made more frequently, and some plants differed by as few as 3 d in their initiation of flowering. Individual plants were relocated during later surveys as they were not removed until the plant had died and was harvested. Death was recorded when the plant had browned, turned brittle, and did not produce more flowers or fruits.

Some plants were grown from natural seedlings, while other plants were grown from experimenter-sown seeds. Seeds were sown to extend germination beyond those germination dates typically realized in nature. The annual seedling emergence experiments are described elsewhere (Kelly and Levin, 1997). Plants grown from experimenter-sown seeds were used for two reasons: (1) Wade and Kalisz (1990) convincingly argued that the application of quantitative methods to measure natural selection was not sufficient to determine why selection operated in the manner observed (they recommended the use of experimental manipulation to identify the agents of viability and fecundity selection as a complement to quantitative analysis), and (2) the experimental randomization of individuals across the environment minimized the correlation of the phenotype with the environment due to past environmental effects, or to the correlation between genotype and environment (Mitchell-Olds and Shaw, 1987).

Ultimately flowering plants grown from natural or experimenter-sown seeds were pooled together for data analysis, as their variables did not differ statistically in any consistent way (Kelly, 1994). Both experi-

mentally derived and naturally derived flowering plants were in the same plots at the same sites; they experienced very similar, if not identical, environments. We studied 3789 flowering plants over a 3-yr period at three sites. In 1990, 209 plants were followed at Montopolis, 136 plants at Bastrop, and 768 plants at Luling. In 1991, 1183 plants were used at Bastrop and 886 plants were surveyed at Luling. In 1992, 607 plants were studied at Bastrop.

Variables measured—Nine life history variables were measured; a description of each is given along with the variable's name. The date each plant initiated flowering was noted (Flowering Date). On dying, or at the end of the fruiting season, all *Phlox* plants in the plots were individually harvested (Death Date). The length of each plant's reproductive adult phase was calculated as the time between its initial flowering date and its death date (Adult Phase). The age at which a plant first reproduced (Age at 1st Reproduction) was determined as the time interval between its germination date and the date blooming was initiated for the first flower cluster to set fruit. Each plant's final dry mass (Mass), the number of flowers, dehiscent fruits, intact fruits, and seeds per intact fruit were measured. Total flowers (Flowers) and total fruits (Fruits) per plant were summed from these values. The proportion of a plant's flowers that formed fruits was its fruit set (Fruit set). The fitness of an individual plant was determined by its total seed set (Fitness); if an individual did not set fruit, its fitness was zero. The number of seeds per flowering plant was estimated by multiplying its total fruits by the average number of seeds per intact fruit on a per-population per-year basis; the number of seeds per fruit was not affected by flowering date (Kelly, 1994). It was necessary to estimate the number of seeds produced per flowering plant as the seed content of dehiscent fruits cannot be determined.

Variation in flowering date and its statistical analysis—The distribution of initial flowering dates was examined for skewness using the g_1 moment statistic (Sokal and Rohlf, 1981, p. 114). This statistic was calculated for each flowering phenology, on a site-by-year basis, using StatView (data analysis software, version 4.1). The significance of this statistic (g_1) was computed using a two-tailed t test with infinite degrees of freedom (Sokal and Rohlf, 1981, pp. 174–175). The null hypothesis that the flowering phenology is symmetrical ($g_1 = 0$) can be rejected when $t_s > 1.960$ ($t_{0.05[\infty]}$). When g_1 is statistically significant and positive, this indicates that the flowering phenology is skewed to the right by plants that initiate flowering late in the season.

Nonparametric tests were applied to the dependent variables when residual analysis showed a significant lack of normality, even for transformed variables, with parametric statistical tests. Since many of the distributions for the variables measured were skewed, nonparametric analyses permitted untransformed data to be examined directly. The effect of flowering date on each of nine life history variables was analyzed with Friedman's two-way nonparametric analysis of variance (ANOVA) with site as a blocking variable. These tests determined whether plants in a population that began to flower at different times differed in the rank distribution for each variable; the critical probability to reject the null hypothesis was <0.05 . A nonsignificant trend was identified when the probability level of correlation was >0.05 but <0.10 .

To provide a systematic view of how life history variables related to initial flowering date, Spearman correlation analysis was used to evaluate their association. To reduce the bias of inadvertently accepting any correlation coefficient as individually significant from a table of correlation coefficients, the sequential Bonferroni technique was used (Rice, 1988). The critical probability levels used were: $P < 0.025$ (Bastrop 1990 and Montopolis 1990) or $P < 0.05$ (Luling 1990, Bastrop 1991, Luling 1991, and Bastrop 1992). A nonsignificant trend was identified when the probability level of correlation was <0.05 but greater than the critical value as determined by the sequential Bonferroni test.

Differences in the likelihood of plants fruiting relative to their initial

flowering dates were tested by the G test. Some flowering dates were combined to have an expected frequency of five or more reproductive plants per cell (Sokal and Rohlf, 1981, p. 709). A minimum number of sequential flowering dates were combined to meet this requirement. The G test determined whether the observed number of reproductive adults for a flowering date differed from the expected number of reproductive adults. The null hypothesis was that the percentage of flowering plants that fruited was equal for all flowering dates.

Flowering date and nonparametric fitness functions—We were motivated to use Schluter's method by the nature of the data itself; the likelihood of reproduction by plants became Poisson distributed as the flowering season progressed. This analytical method was able to deal with this aspect of the data's distribution satisfactorily (D. Schluter, personal communication; Schluter, 1988). A smoothing parameter was identified, which minimized the sum of the squared deviations between the observed fitness values and the estimated fitness values. The predicted fitness for a plant was calculated for each flowering day. The flowering day was calculated as the number of days between a given plant's initial flowering date and the first calendar date that any plant flowered at that site in that year. The variance between the mean of the squared deviations among plants in their predicted fitness from the average predicted fitness of all plants was calculated. Though Schluter (1988) characterized the overall intensity of natural selection by this variance in predicted fitness, we will not refer to the fitness variance as selection intensity. This is to avoid confusion with another measure of selection intensity that is measured as the average of the absolute deviations of each individual from the maximum fitness.

Bootstrap resampling of each flowering day's predicted fitness was used to determine the mean predicted fitness for each flowering day and its standard error. This was done to reduce any bias in the fitness function caused by its smoothness, where the slope of the true fitness function might change abruptly (Schluter, 1988). The 1000 replicate bootstrap regressions were performed on randomly resampled data. The bootstrap-generated Poisson random fitness values for each flowering day based on the estimated fitness value and the distribution of errors found in the data (Schluter, 1988). These replications were done using the smoothing parameter that best minimized the sum of the squared deviations between the observed fitness values and the estimated fitness values.

For descriptive purposes, an exponential curve ($y = ae^{bx}$) was fitted to the mean predicted values of fitness (y) vs. flowering day (x). This function was selected after viewing the plot of mean predicted fitness vs. flowering day. The multiple correlation coefficient (R) was used to measure the level of the association between the predicted fitness and flowering day. Linear and polynomial functions were also evaluated in addition to the exponential function. The linear and polynomial functions fitted to the predicted values of fitness (y) vs. flowering day (x) had smaller R than those determined using an exponential function.

RESULTS

The distribution of flowering was skewed to the right in all years and populations by the occurrence of plants that initiated flowering late in the season. The skewness statistic (g_1), sample t statistic (t_s), and associated probability (P) were: 1990—Bastrop ($g_1 = 0.937$, $t_s = 4.461$, $P < 0.001$), Luling ($g_1 = 0.705$, $t_s = 7.976$, $P < 0.001$), and Montopolis ($g_1 = 0.394$, $t_s = 2.325$, $0.01 < P < 0.05$); 1991—Bastrop ($g_1 = 1.835$, $t_s = 25.766$, $P < 0.001$) and Luling ($g_1 = 0.649$, $t_s = 7.882$, $P < 0.001$); and 1992—Bastrop ($g_1 = 0.288$, $t_s = 2.897$, $0.001 < P < 0.01$). In addition, there were differences among years and populations in the location of the peak in natural flowering and in the length of the flowering season (Figs.

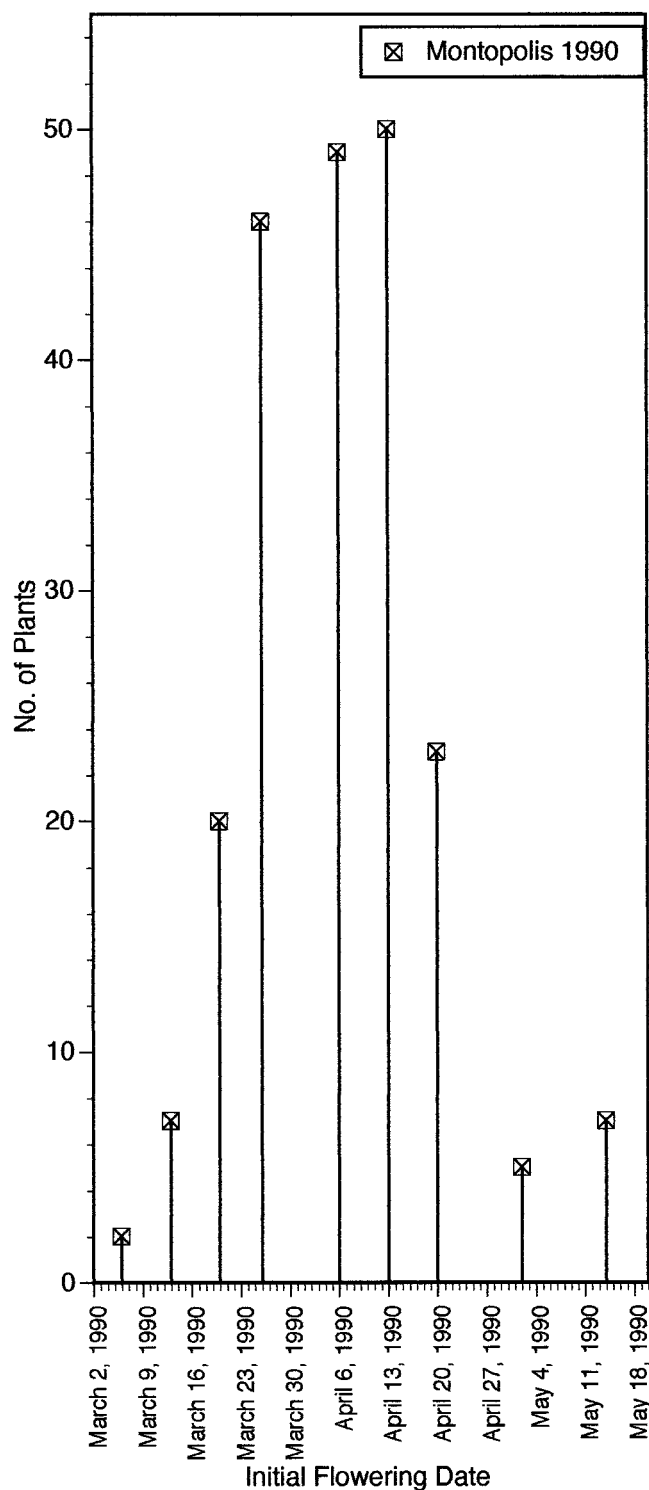


Fig. 1. The phenology of flowering at Montopolis in 1990.

1–3). In 1990, plants began to flower in late February and continued into late May at three sites (Figs. 1–3). Flowering occurred over a 48–69 d period. First flowering occurred as late as 14 May at Bastrop and Montopolis. The peak in the initiation of flowering occurred in mid-March at Luling, mid-April at Montopolis, and late April at Bastrop. In 1991, flowering occurred over a lon-

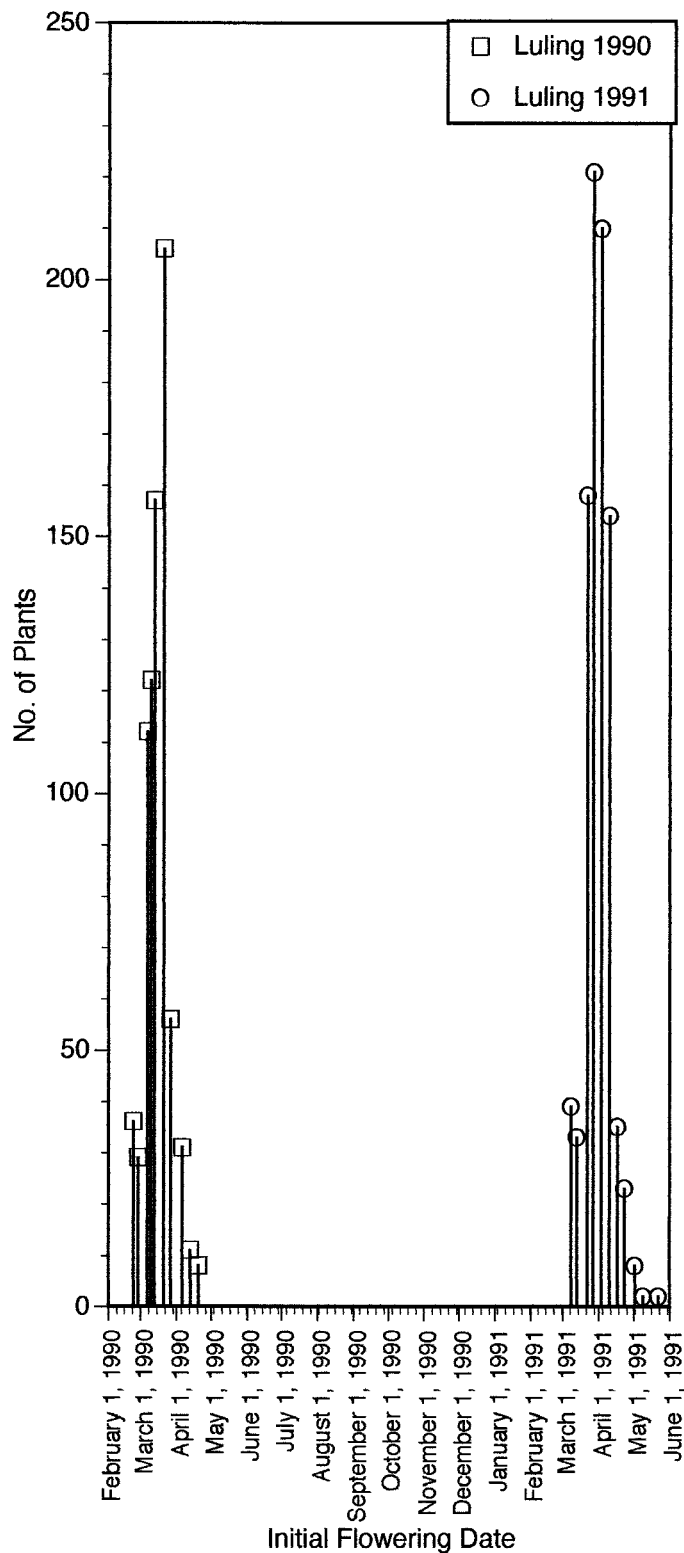


Fig. 2. The phenology of flowering at Luling in 1990 and 1991.

ger time, generally beginning in March (with the exception of one plant flowering and dying in late December at Luling) and continuing through late May (Figs. 2–3). At Bastrop, the peak in first flowering was in early April, while at Luling this peak occurred in late March. Flow-

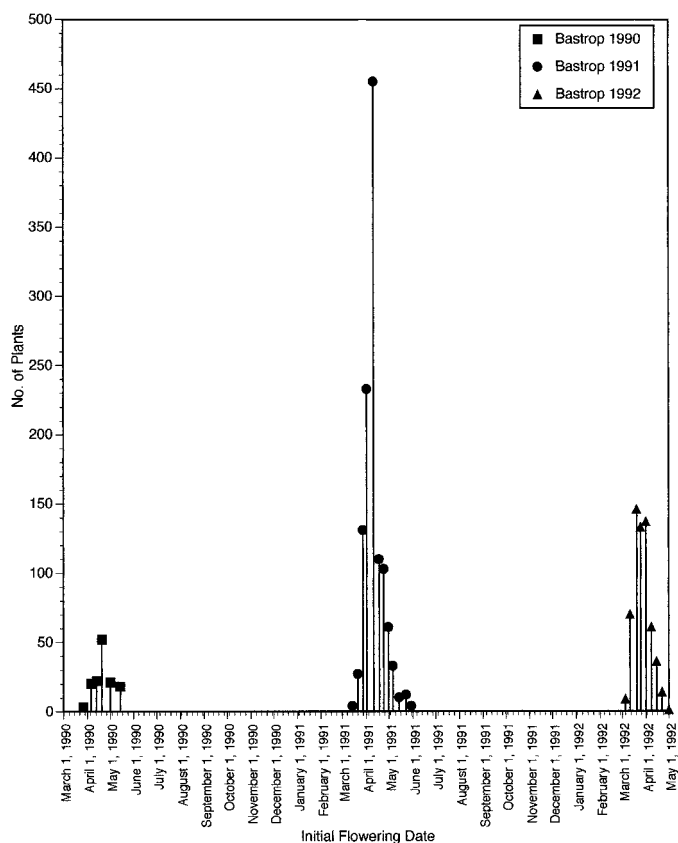


Fig. 3. The phenology of flowering at Bastrop in 1990, 1991, and 1992.

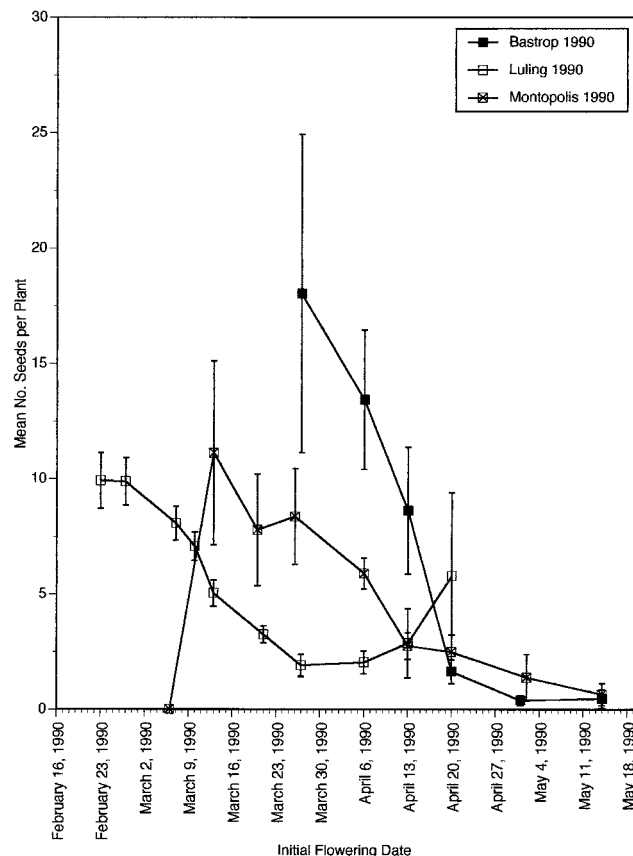


Fig. 4. For 1990, the mean number of seeds set by a flowering plant (± 1 SE) per flowering date at Bastrop, Luling, and Montopolis.

ering occurred over 74–77 d. The flowering season began in mid-March at Bastrop and early March at Luling; it continued through late May at both sites. In 1992, flowering at Bastrop was limited to a 57-d period, from early March to early May (Fig. 3). The peak in first flowering was in late March, just 15 d after the first plants flowered.

In 1990, at Bastrop, some plants from every flowering date censused produced seeds (Fig. 4); the highest mean fitness was achieved by the first flowering plants, which began to flower ~ 24 d before most plants initiated flowering. Though 40% of 136 flowering plants produced seeds, the 91 plants that began to flower during the last 24 d of the flowering season typically failed to make more than three seeds per plant. Similarly at Luling, plants that initiated flowering 18 d before most plants flowered had the highest fitness (Fig. 4). Though 66% of 768 flowering plants produced seeds, and some plants from every flowering date censused reproduced, only the 98 plants that began to flower at the end of the flowering season (during the last 7–24 d) typically failed to make more than three seeds per plant. At Montopolis nine flowering dates were monitored and eight of these included plants that produced seeds (Fig. 4). Plants that began to flower 31 d before the peak in initial flowering achieved the highest fitness. Though 70% of 209 flowering plants produced seeds, the 35 plants that began to flower during the last 24 d of the flowering season typically failed to set more than three seeds per plant.

In 1991, at Bastrop, those plants that began to flower

first, 28 d before the peak flowering date, were the most fit (Fig. 5). Though some plants from every flowering date censused reproduced, only 41% of 1183 flowering plants fruited. The 772 plants that began to flower in the last 16–49 d of the flowering season typically failed to produce more than three seeds per plant. At Luling, the highest fitness was measured for those plants that began to flower 19 d before the peak in the initiation of flowering (Fig. 5). Though some plants from eight of the 12 flowering dates censused reproduced, only 31% of 886 flowering plants produced seeds. The 813 plants that began to flower during the last 61 d of the flowering season typically failed to set more than three seeds per plant.

In 1992 at Bastrop, plants that initiated flowering ~ 15 d before the population's peak in first flowering were the fittest (Fig. 6). Though some plants from every flowering date censused were reproductive, only 49% of 607 flowering plants produced seeds. The 249 plants that began to flower during the last 30 d of the flowering season typically did not make more than three seeds per plant.

A *Phlox* plant's initial flowering date had a significant effect on all life history variables measured: the plant's Death Date, the length of a plant's reproductive Adult Phase, the Age at 1st Reproduction, the total number of Flowers and the total number of Fruits per plant, the proportion of a plant's flowers that formed fruits (Fruit set), a plant's final dry Mass, and the Fitness of an individual plant (Table 1).

In five of the six separate population by year combi-

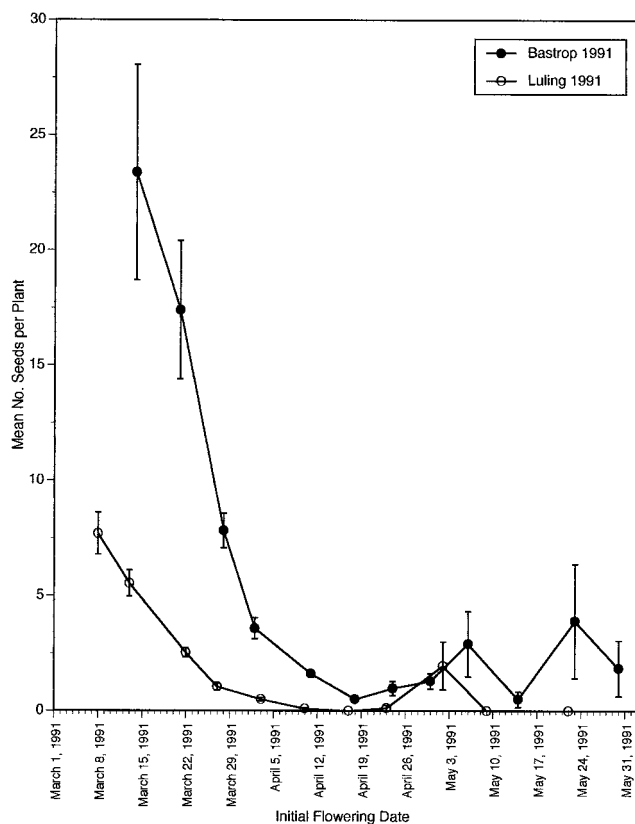


Fig. 5. For 1991, the mean number of seeds set by a flowering plant (± 1 SE) per flowering date at Bastrop and Luling.

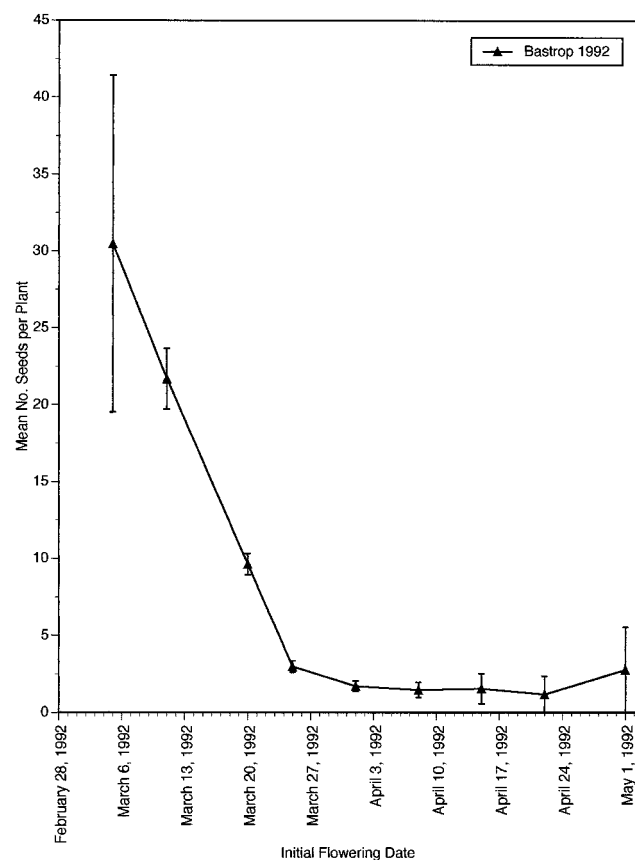


Fig. 6. For 1992, the mean number of seeds set by a flowering plant (± 1 SE) per flowering date at Bastrop.

nations studied, the likelihood of a plant reproducing was significantly affected by its initial flowering date. In 1990, plants that flowered after 13 March at Luling ($G = 36.877$, $df = 8$, $P < 0.001$) and 13 April at Bastrop ($G = 20.844$, $df = 3$, $P < 0.001$) experienced a reduction in the frequency of reproduction (below 66% and 40% respectively, if the likelihood of reproduction was equal across flowering dates). This relationship was not significant at Montopolis (1990) where $>70\%$ of all flowering plants reproduced ($G = 8.598$, $df = 5$, $P > 0.05$). In 1991, the inequality in reproduction relative to flowering date was more strongly expressed than the previous year. All plants that flowered after 22 March at Luling and 2 April at Bastrop had a highly reduced level of reproduction. This was evident at Luling ($G = 201.469$, $df = 5$, $P < 0.001$) and Bastrop ($G = 113.163$, $df = 7$, $P < 0.001$) if fruiting was equal across flowering dates (31 and 41%, respectively). In 1992 at Bastrop, the only population studied, all plants that flowered after 20 March had a reduced frequency of reproduction (below the 49% expected). Thus the likelihood of reproduction was significantly affected by flowering date ($G = 108.334$, $df = 5$, $P < 0.001$).

Significant positive correlations with flowering date were generally observed for death date and age at first reproduction (Tables 2–4). In marked contrast, significant negative correlations with flowering date were always observed for the duration of a plant's adult phase and its final mass in all populations and all years (Tables 2–4). Similarly, total flowers and total fruits always decreased

with later flowering date in all years and at all sites. Though, individual fitness was always negatively correlated with flowering date; the proportion of a plant's flowers that formed fruits was negatively correlated with flowering date in only four of the six populations studied (Tables 2–4).

Generally, flowering plants were predicted to produce an average of 3.87 seeds across all flowering dates surveyed at three sites. In four populations, Bastrop (1990), Luling (1990), Montopolis (1990), and Bastrop (1992) a flowering plant was predicted to produce more than 4.51 seeds. In

TABLE 1. Friedman's two-way nonparametric ANOVA testing for differences between the distribution of life history variables based on the initial flowering date. Population was used as the blocking variable when initial flowering date was tested as the main effect.

Variable	df	χ^2	P
Death Date	23	31 284	***
Adult Case	23	1 746 118	***
Age at 1st Reproduction 1991	15	3 598	***
Age at 1st Reproduction 1992	5	5 863	***
Flowers	20	321 128	***
Fruits	18	149 613	***
Fruit set	18	115 058	***
Mass	19	254 522	***
Fitness	23	469 863	***

Note: Trend = $0.05 < P < 0.1$; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

TABLE 2. For 1990, Spearman correlation analysis of life history variables (number of flowering plants) with initial flowering date. The sequential Bonferroni test was applied; P_{critical} is the level of significance used (Rice, 1988).

Population	Variable	r	P
Bastrop 1990	Death Date (136)	-0.0068	$P_{\text{critical}} < 0.025$
	Adult Phase (136)	-0.9920	ns
	Flowers (126)	-0.5616	0.0001
	Fruits (55)	-0.6539	0.0001
	Fruit set (55)	-0.2704	trend
	Mass (119)	-0.5706	0.0001
	Fitness (136)	-0.5503	0.0001
Luling 1990	Death Date (768)	0.0967	$P_{\text{critical}} < 0.05$
	Adult Phase (768)	-0.9326	0.0073
	Flowers (741)	-0.2695	0.0001
	Fruits (505)	-0.3517	0.0001
	Fruit set (505)	-0.3088	0.0001
	Mass (691)	-0.2641	0.0001
	Fitness (768)	-0.4156	0.0001
Montopolis 1990	Death Date (209)	0.0749	$P_{\text{critical}} < 0.025$
	Adult Phase (209)	-0.9797	ns
	Flowers (193)	-0.3589	0.0001
	Fruits (147)	-0.3589	0.0001
	Fruit set (147)	-0.0627	0.0001
	Mass (181)	-0.3305	ns
	Fitness (209)	-0.3968	0.0001

two populations, Bastrop (1991) and Luling (1991), a flowering plant was predicted to set three seeds or fewer per plant. Fitness declined as the plants began to flower later in the season in all populations. Nonparametric fitness functions were determined for each population sampled on a yearly basis. The pattern of the decline in fitness was nonlinear (Fig. 7). For descriptive purposes, the exponential functions and their R^2 's are given in Table 5. The mean predicted fitness per flowering day ultimately

TABLE 3. For 1991, Spearman correlation analysis of life history variables (number of flowering plants) with initial flowering date. The sequential Bonferroni test was applied; P_{critical} is the level of significance used (Rice, 1988).

Population	Variable	r	P
Bastrop 1991	Death Date (1181)	0.2159	$P_{\text{critical}} < 0.05$
	Adult Phase (1181)	-0.5907	0.0001
	Age at 1st Reproduction (118)	0.3321	0.0002
	Flowers (1139)	-0.3390	0.0001
	Fruits (485)	-0.3924	0.0001
	Fruit set (485)	-0.1881	0.0001
	Mass (221)	-0.4825	0.0001
	Fitness (1185)	-0.4084	0.0001
Luling 1991	Death Date (885)	0.1404	$P_{\text{critical}} < 0.05$
	Adult Phase (885)	-0.9330	0.0001
	Age at 1st Reproduction (70)	0.2843	0.0171
	Flowers (862)	-0.3842	0.0001
	Fruits (271)	-0.3861	0.0001
	Fruit set (271)	-0.1288	0.0001
	Mass (100)	-0.3765	0.0001
	Fitness (886)	-0.5584	0.0001

TABLE 4. For 1992, Spearman correlation analysis of life history variables (number of flowering plants) with initial flowering date. The sequential Bonferroni test was applied; P_{critical} is the level of significance used (Rice, 1988).

Population	Variable	r	P
Bastrop 1992	Death Date (607)	0.2526	$P_{\text{critical}} < 0.05$
	Adult Phase (607)	-0.4623	0.0001
	Age at 1st Reproduction (142)	0.2630	0.0016
	Flowers (590)	-0.5496	0.0001
	Fruits (296)	-0.4938	0.0001
	Fruit set (296)	-0.3214	0.0001
	Mass (551)	-0.4742	0.0001
	Fitness (607)	-0.6197	0.0001

declined as plants began to flower later in the season. For all six populations the very first flowering plants had the highest predicted mean seed set, all subsequent flowering plants had reduced mean seed set (Fig. 7).

The strength of selection on flowering date in *Phlox* varied in magnitude among sites in all years and among years within sites (Fig. 7). For example, the rate of decline in fitness was very shallow at Montopolis (1990), falling 50% in 23 d, whereas at Bastrop (1991) it was very steep, falling 50% in 6 d. Similarly, fitness functions were not uniform in scale at Bastrop over three consecutive years (1990–1992). In four populations (Luling 1990, Bastrop 1991, Luling 1991, and Bastrop 1992) there were slight increases in mean predicted fitness for

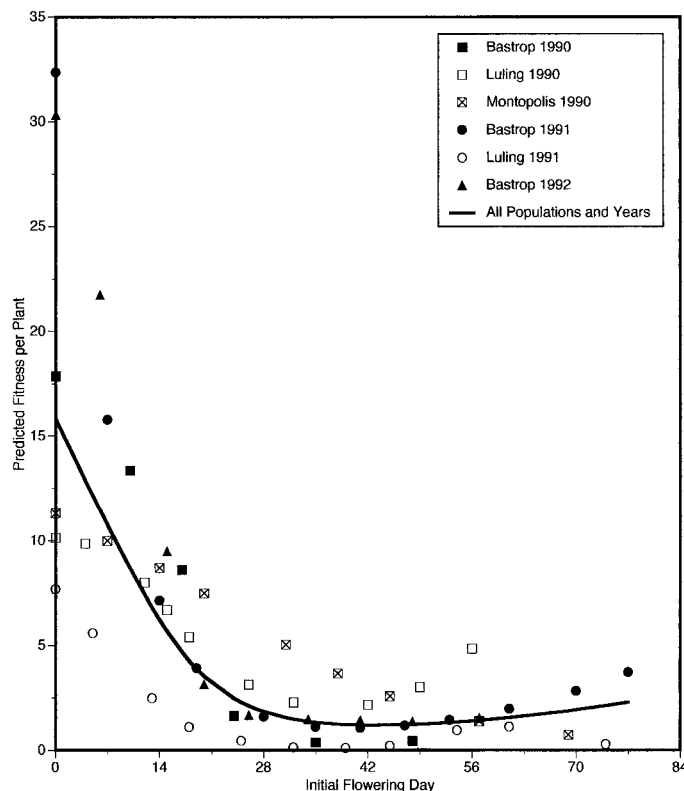


Fig. 7. The scatterplot of predicted mean fitness (y, mean number of seeds) per initial flowering day (x) at Bastrop, Luling, and Montopolis (1990–1992).

TABLE 5. The exponential fit ($y = ae^{bx}$) of predicted mean fitness (y) per flowering day (x) at Bastrop, Luling, and Montopolis (1990–1992), with their associated exponential curve coefficients and multiple correlation coefficient (R) with $N-2$ degrees of freedom. N = the number of flowering dates.

Years	Population	a	b	R	df	P
1990	Bastrop	23.22730	−0.09407673	0.940	4	**
1990	Luling	8.58594	−0.02298002	0.750	8	*
1990	Montopolis	14.50329	−0.04023612	0.986	7	**
1991	Bastrop	8.66978	−0.02691169	0.610	10	*
1991	Luling	2.55054	−0.03686649	0.600	9	Trend
1992	Bastrop	18.30594	0.05777666	0.884	7	**
1990–1992	All	7.28449	0.02985441	0.765	38	**

Note: Trend = $0.05 < P < 0.1$; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

plants that began to flower during the last 39–77 d of the flowering season; however, the predicted fitness for any of these late flowering plants averaged only 1.59 seeds. The fitness variance among flowering dates ranged from 3.248 to 50.059 (seeds/individual)² (Table 6). This variance in fitness differed among sites in all years and among years within sites.

DISCUSSION

The length of the flowering season for any *Phlox drummondii* population is unpredictable; there was no relation between a month's total rainfall and the month of the flowering season ($r = 0.26$, $N = 17$) (NOAA, 1990, 1991, 1992). Over 3 yr at Bastrop for example, there was as much as a 22-d difference in the start of the flowering season and as much as a 29-d difference in the end of the flowering season. Cohen (1976) modeled the reproduction of annuals in a habitat where the length of the flowering season was unpredictable; he proposed that to insure some seed production in all years, plants should begin flowering earlier and over a longer span of time (i.e., the adult phase). In *Phlox*, plants that flowered earlier also tended to reproduce at a younger age and spend more time in the reproductive adult phase than did later flowering plants. A similar relation has been established in *Plantago major*, where plants (in one population) that flowered earlier also reproduced at a younger age (Lotz, 1990), and *Linanthus androsaceus*, where the duration of the adult phase was dependent on plant size (Schmitt, 1983).

The mean seed set per plant fell markedly as *Phlox* plants initiated flowering later in the season. The earliest flowering plants (in the first 10 d of the season) had the highest average fitness. In contrast, those plants that began to flower at the peak of the flowering season (~30 d later) had more than a fourfold reduction in mean fit-

ness and produced offspring below the replacement rate. The fitness advantage of early flowering has also been demonstrated for *Claytonia virginica* and *Erythronium albidum* (Schemske et al., 1978), *Leptospermum scoparium* (Primack, 1980), *Solidago juncea* (Gross and Werner, 1983), *Spartina anglica* (Mullins and Marks, 1987), *Glycine max* (Lin and Nelson, 1988), *Plantago major* (Lotz, 1990), *Viscaria vulgaris* (Kwak and Jennersten, 1991), and *Geranium maculatum* (Agren and Willson, 1992).

Phlox has a positively skewed flowering phenology like many annual plants: *Arabidopsis thaliana* (Jones, 1971); *Androsace septentrionalis*, *Draba nemorosa*, and *Gentiana amarella* (Thomson, 1980); *Linanthus androsaceus* (Schmitt, 1983); and *Impatiens capensis* (Schmitt, Eccleston, and Ehrhardt, 1987). Flowering began abruptly, peaked rapidly, and declined gradually over time. This phenological pattern is typical of many temperate plants and is independent of their pollination syndrome (Gentry, 1974; Rabinowitz et al., 1981). *Phlox* plants that flowered earlier in the year also tended to die earlier in the year. Similar correlations between phenologies have been found for many annual (*Avena barbata*, *Brassica nigra*, *Bromus tectorum*, *Collinsia childii*, *Cryptanthus intermedia*, *Gilia tenuiflora*, *Phacelia curvipes*—Slade, 1975), biennial (*Daucus carota*—Lacey, 1982), and perennial species (*Asclepias*—Kephart, 1987; *Senecio integrifolius*—Widen, 1991a).

In five of six instances (populations by year) the likelihood of reproduction by *Phlox* plants was significantly related to flowering date. Earlier flowering *Phlox* plants were typically larger than later flowering plants. The association between flowering date and size has also been observed for *Astragalus sabulonum*, *Baileya pleniradiata*, *Camissonia brevipes*, *Chaenactis carphoclinia*, *Oenothera deltoidea*, *Phacelia crenulata*, and *Plantago insularis* (Bell, Hiatt, and Niles, 1979), and *Chamaecrista fasciculata* (Kelly, 1992). In annuals, a plant's reproductive performance is positively correlated with its mass (Schmitt, 1983; Schmitt, Eccleston, and Ehrhardt, 1987). As *Phlox*'s average mass declined along with later flowering, so did the number of flowers, fruits, and fruit set (in four populations) decline. Late-flowering *Phlox* plants flowered at a younger age and in greater synchrony with the population than might be expected based on the extended range of germination dates. However, this was not sufficient to overcome the penalty of late flowering on total flower and fruit production. Consequently, seed set was strongly affected by flowering date. Similar seasonal decreases in the number of flowers per plant (*Cynoglos-*

TABLE 6. Variance (seeds/day)² among plant's initial flowering dates in their predicted fitness.

Year	Population	Fitness variance
1990	Bastrop	26.563
1990	Luling	5.754
1990	Montopolis	5.857
1991	Bastrop	10.427
1991	Luling	3.248
1992	Bastrop	50.059
1990–1992	All	10.234

sum officinale—De Jong and Klinkhamer, 1991), fruits per plant (*Spartina anglica*—Mullins and Marks, 1987), and fruit set per plant (*Leptospermum scoparium*—Primack, 1980; *Geranium maculatum*—Agren and Willson, 1992) relative to flowering date have been noted.

The fitness functions demonstrate that early flowering was consistently at a selective advantage from among the broad range of flowering dates in *Phlox*. The earliest flowering plants always had the highest predicted fitness. In *Senecio integrifolius*, plants that initiated flowering in the first 10 d of the season had the highest fitness in a majority of years Widen (1991a). There the fitness surface was concave and decreasing, with maximum fitness realized by early flowering plants. Though the fitness functions for *Senecio* failed to always indicate directional selection for early flowering, plants that initiated flowering after the population's peak in flowering were always selected against (Widen, 1991a).

The fitness functions that describe *Phlox*'s seasonal decline in seed set are nonlinear in all populations studied. Similar results were found in *Senecio* by Widen (1991a) where six of eight fitness functions for flowering date were nonlinear. Nonlinearity in fitness functions indicates that the fitness penalty due to later initiation of flowering is not constant over time. In *Phlox* the penalty for plants that began to flower in the first 14 d was a loss of 0.43 seeds per day's delay in first flowering (i.e., one fruit per week). The penalty for plants that began to flower in the last 21 d of the season, in addition to their 75% reduction in total seed set, was a loss of 0.04 seeds per day's delay in initial flowering (i.e., one fruit per 9 wk).

We determined that the strength of selection on flowering date in *Phlox* varied in magnitude among sites in all years and among years within sites. Other studies that have used multiple sites to estimate the fitness effects of flowering date have similarly observed that the intensity of selection varied both among sites and within sites (Stewart and Schoen, 1987; Widen, 1991b; Kelly, 1992). It is important to recognize that fitness functions also serve as an historical portrait of phenotypic selection on flowering day. Though the strength of selection for early flowering in *Phlox* was typically great, it is striking how consistent the fitness functions were in "shape" across sites and years when the nonparametric method makes no a priori assumptions about what function to fit to the data. This suggests that the variability that *Phlox* experiences in selection on flowering date is variability in the intensity of selection rather than in the kind of selection.

The pattern of phenotypic selection for early flowering cannot be used by itself to predict the evolutionary response to selection. The evolutionary response depends not only on the direction and intensity of selection, but also on genetic variability for this trait and other genetically correlated traits. Though a genetic basis for flowering time has been demonstrated in many plant species (e.g., *Lolium temulentum*—Cooper, 1959; *Melandrium album* and *M. rubrum*—Lawrence, 1963; *Mimulus cardinalis* and *M. lewisii*—Hiesey, Nobs, and Bjorkman, 1971; *Glycine max*—Lin and Nelson, 1988; *Senecio integrifolius*—Widen, 1991a) and flowering time has been modified by artificial selection in *Zea mays* (Paterniani, 1969; Troyer and Larkin, 1985), *Limnanthes alba* (Jain, 1979), *Plectris brachystemon* and *P. congesta* (Carey,

1983), nothing is known about the genetic basis for the individual variation observed in *Phlox*'s flowering time. It is suggestive that little or no heritability has been found in *Phlox* for a germination trait (a correlated phenology) under similar strong, directional selection (Kelly and Levin, 1997). Similarly low heritabilities for life history traits have been measured in natural populations of *Phlox* and other plant species (Mitchell-Olds, 1986; Schwaegerle and Levin, 1991; Platenkamp and Shaw, 1992; Stratton, 1992). The potential exists that after many generations of directional selection for early flowering in *Phlox*, little evolutionary response to added phenotypic selection for early flowering could result.

Schmitt (1983) determined that as plant density increased, the degree to which flowering phenology was skewed increased, and Augspurger (1981) observed that flowering plant density was associated with the number of pollinators attracted to a site. These two phenomena, which are not mutually exclusive, may underlie the fitness advantage realized by *Phlox* plants that initiated flowering early in the season. *Phlox* plants that initiate flowering when flowering plant density is at its lowest are likely the most conspicuous and attractive to pollinators, and consequently they received the highest level of service. This line of reasoning is sensible if the fitness achieved by these flowering plants is determined more strongly by limitation in the number of pollinators rather than physical resources. Two pieces of evidence support our speculation that the number and behavior of pollinators largely determine fitness (in this instance). Field notes record the presence of butterflies on *Phlox* only once out of 66 survey dates during three flowering seasons (Kelly, unpublished data). Secondly, Plitmann and Levin (1996) demonstrated that hand pollination of *Phlox* flowers in the field (to supplement insect pollination) doubled fruit set in six natural populations from 44.29 to 95.03% (weighted averages; Plitmann and Levin, 1996). While it may be that early flowering is typically favored in *Phlox*, it does not follow that the first flowering plants will always have the highest fitness. What is generally evident is that the first flowering plants disproportionately contribute many offspring to the next generation, followed by an "exponential" decline in fitness for plants that begin to flower later in the season.

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